On the polytypic and problematic Clausilia dubia: notes on its nomenclature and systematics (Gastropoda, Pulmonata, Clausiliidae)

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The nomenclature of some subspecies of Clausilia dubia is changed on the basis of type material studied and the synonymy is revised accordingly. The subspecies generally known as C. d. obsoleta should be called C. d. dubia instead. The name C. d. vindobonensis has to be used for the taxon usually considered the nominate subspecies by recent authors. An alpine subspecies, C. d. alpicola, is preliminary re-described and figured. Altitudinal variation as known from the Austrian eastern Alps, but differing in various aspects, is described for populations of C. dubia from the Val di Funes (Villnösstal) in the southeastern Alps of Italy.

Key words: Gastropoda, Pulmonata, Clausiliidae, Clausilia, subspecies, clines, nomenclature, Italy, Austria.

INTRODUCTION

Variation within the species Clausilia dubia Draparnaud, 1805, is extremely heterogeneous. Next to several well-defined local subspecies and two ill-defined wide-spread ones, there are obvious altitudinal clines in relatively small areas of its range, contrasting with series of populations in which there is no significant correlation between shell morphology and altitude. To explain the morphological and distributional patterns, Klemm (1960) suggested a complicated evolutionary scenario for the Austrian taxa. He hypothesized the occurrence of two large groups of populations during Pleistocene glaciations, north of the Alps and along the eastern border, respectively. In addition he assumed the survival of small, local populations along the Alpine border and on nunataks amidst the ice during those cold periods, whereas in warmer times many distributional gaps were filled again by dispersing snails, resulting in secondary contacts between more or less differentiated populations. This hypothetical, dynamic scenario is based on morphological data and distributional patterns and is not contradicted by geological data. It deserves to be tested with e.g. molecular methods. Similar evolutionary histories have been suggested for other E-Alpine polytypic gastropod species, such as e.g. Macrogastra badia (C. Pfeiffer, 1828), Neostyriaca corynodes (Held, 1836), Trichia [s. lat.] spec. and Arianta arbustorum (Linnaeus, 1758) (Klemm, 1974; Gittenberger, 1991).

This paper concerns (1) a confusing but inevitable correction of the nomenclature of two well-known subspecies of *C. dubia*, with a revision of the synonymy, (2) a preliminary re-description of an Alpine subspecies which might have evolved on Pleistocene nuna-

taks, and (3) the description of a peculiar case of altitudinal variation, differing from clinal variation known from eastern Austria.

MATERIAL AND METHODS

Material from several collections was investigated (see the list of abbreviations). To be able to stabilize the use of names, type specimens were studied whenever possible. Only shell characters could be taken into account. When localities are listed, the provinces are arranged alphabetically, whereas the localities are ordered according to their UTM code numbers.

Abbreviations used for collections: FSM, Florian Schrott, 'Bischöfliches Seminar Johanneum', Dorf Tirol near Merano; HMK, H. P. M. G. Menkhorst, Krimpen aan de IJssel; MZUF, Museo di Zoologia dell'Università di Firenze; NHMW, Naturhistorisches Museum Wien; NMB, Naturhistorisches Museum Bern; NNM, Nationaal Natuurhistorisch Museum, Leiden; NNM-V, L. A. W. C. Venmans in NNM; RBH, R. A. Bank, Hoofddorp; WFW, W. Fauer, Winterstein; WMD, W. J. M. Maassen, Duivendrecht; WNH, W. H. Neuteboom, Heemskerk (now in NNM); ZMB, Zoologisches Museum Berlin.

RESULTS AND DISCUSSION

(1) The nominal taxa Clausilia dubia dubia and C. d. obsoleta

A footnote in a paper on the genus Clausilia by H. Nordsieck (1990: 145) has farreaching consequences for the nomenclature of some wide-spread and frequently cited European subspecies of C. dubia. On the basis of type specimens studied, we can only confirm that the nominate subspecies has been incorrectly referred to as C. d. obsoleta A. Schmidt, 1856, by Klemm (1960), whereas the taxon indicated by that author as C. d. dubia should be named C. d. vindobonensis A. Schmidt, 1856. We see no escape from these confusing changes in nomenclature. Revised synonymy lists for the two nominal taxa are given below.

The two subspecies in question, though accepted as such by many authors, cannot always be distinguished easily. There is no distinct hybrid zone between clearly separate morphological entities. Intermediate forms are relatively wide-spread. In the revised sense, C. d. dubia is most clearly characterized by the, in front view, rather vaguely stepped profile of the columellar lamella, whereas that lamella seems to be prominently doubled at its anterior end in C. d. vindobonensis. See also Klemm (1960).

Genus Clausilia Draparnaud, 1805; subgenus Andraea L. Pfeiffer, 1848

Clausilia (Andraea) dubia dubia Draparnaud, 1805 (figs 1, 3-6, 8, 9, 19)

Clausilia dubia Draparnaud, 1805: 70, pl. 4 fig. 10. Lectotype (design. nov.): NHMW, Colln Draparnaud 1820.XXVI.75a (fig. 5). Type locality: unknown.

Glischrus (Clausilia) roscida S. Studer, 1820: 89 (in reprint: 20). Lectotype (design. Forcart, 1957: 193, pl. 3 fig. 19): NMB, Colln Studer/Perry 48.79 (figs 1, 3). Type locality: Switzerland, "Berner Jura".

Clausilia dubia var. obsoleta A. Schmidt, 1856: 40, 44, pl. 5 figs 90, 91, 93, pl. 10 fig. 196. Lectotype (design.

Kilias, 1974: 191): ZMB 101709 (the specimen figured by A. Schmidt, 1856: fig. 91). Type locality: Switzerland, "Via Mala in Graubünden".

Clausilia dubia var. sordellii Adami, 1876: 66, pl. 1 figs 10-13. Syntypes: MZUF/3 & 15 shells, all from "Borno", ex Adami. Type locality: Italy, province of Brescia, "unicamente a Borno (1000) sotto il ponte dell'Uscio nelle corteccie dei salici".

Clausilia dubia var. reticulata Pini, 1883: 141. Syntypes unknown; according to Soika (1950: 225) the Colln Pini has been destroyed. Type locality: Italy, province of Sondrio, "Le Prese Vallis Tellinae" (Valtellina).

Clausilia dubia var. langobardica Pini, 1883: 143. Syntypes unknown (see above). Type locality: "parte settentrionale d'Italia" (western Italy).

Notes on the literature. — While describing *Clausilia dubia*, Draparnaud (1805: 70) mentioned no locality. This resulted in some amazingly contradictory statements in the literature.

Bourguignat (1877: 20) commented: "Il est probable que les échantillons de Draparnaud ont été receuillis aux environs de Crest, dans les alluvions de la Drôme. On sait en effet que la savant auteur de la première Malacologie Française a passé plusieurs étés dans cette petite ville du Dauphiné". [The samples of Draparnaud have probably been collected near Crest, along the Drôme. It is known indeed that the wise author of the first M. F. has spent several summers in this small city of the Dauphiné].

Forcart (1957: 199) wrote: "Vermutlich begründete Draparnaud .. Clausilia dubia auf Gehäusen die er durch Faure Biguet aus der Sammlung von S. Studer erhielt, so dass der Originalfundort 'Berner Jura' von Glischrus (Clausilia) roscida mit demjenigen von Clausilia dubia identisch ist"). [Draparnaud probably based C. d. on shells received from Faure Biguet from the S. Studer collection, consequently the original locality 'Berner Jura' of G. (C.) roscida is identical with that of C. dubia].

Klemm (1960: 83) wrote: "Es unterliegt kaum einem Zweifel, dass Draparnaud .. die vorliegende .. Clausilie vor sich hatte.. Dafür spricht die Beschreibung, die Tatsache, daß Draparnaud aus dem fraglichen Gebiete Material bezog, vor allem aber die Prüfung der im Wiener Naturhistorischen Museum liegene Originalstücke". [It can hardly be doubted, that Draparnaud had this clausiliid before him. In favour of this view are the description, the fact that Draparnaud received specimens from the area in question, and in particular the study of the original specimens in the Viennese Museum of Natural History].

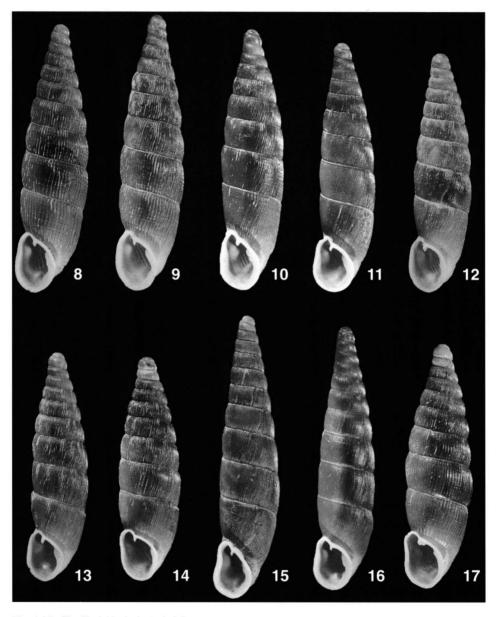
H. Nordsieck (1990: 145) finally stated, in striking contrast with Klemm (1960): "Die Untersuchung des Originalexemplars von dubia .. zeigte, daß es sich um eine obsoleta handelt". [The investigation of the original specimen of dubia showed that it concerns an obsoleta]. According to H. Nordsieck (1990: 145, footnote), Glischrus (Clausilia) roscida S. Studer, 1820, differs from Clausilia dubia obsoleta A. Schmidt, 1856.

Type series. — In the Museum of Natural History in Vienna (NHMW), the Colln Draparnaud contains a single sample labelled 'Clausilia dubia' (no. 1820.XXVI.75a), without a locality indicated, with one shell belonging to C. dubia and two of C. nugsa parvula (A. Férussac, 1807). This is in agreement with a report on the Draparnaud collection published by Locard (1895: 91). Apparently nothing has changed during a century. The specimen formally selected now as the lectotype of C. dubia, belongs to the subspecies indicated as C. dubia obsoleta by Klemm (1960) and following authors. The apertural characters are typical for that subspecies, whereas the shape of the shell is less slender than usual and its sculpture is relatively fine.

The type series of Glischrus (Clausilia) roscida S. Studer, 1820, in NMB, Colln S. Studer/M. Perry (no. 48.79) contains five shells. The two original labels, in Perry's handwriting,



Figs 1-7. Clausilia dubia. 1, 3-6, C. d. dubia; 2, 7, C. d. vindobonensis. 1, 3, 4, Glischrus (Clausilia) roscida: 1, 3, lectotype (height 12.5 mm) and 4, paralectotype (height 11.6 mm). 5, C. d. dubia, lectotype (height c. 10.7 mm) [photograph provided by Dr. K. Edlinger]. 6, C. dubia var. obsoleta, paralectotype (height 11.2 mm). 2, 7, C. dubia var. vindobonensis type series without lectotype (2), and paralectotype (7, height 11.8 mm). See the text for locality data and collections. Photographs, except 5, by Bank.



Figs 8-17. Clausilia dubia. 8, 9, C. d. dubia, Italy, Bozen (Bolzano), Pragser Wildsee (Lago di Braies), 1500 m, E.G. leg. (height 12.6 and 12.8 mm, respectively). 10-14, C. d. alpicola. 10, 11, Belluno, E-side of Andraz, westfoot Monte Pore, 1300-1400 m alt., E.G. leg. (height 12.1 and 11.6 mm, respectively); 12, Trento, between Predazzo and Moena, A. & E.G. leg. (height 11.1 mm); 13, Trento, E-side Passo di Sella, 3.5 km NNE of Canazei, 1900 m alt., E.G. leg. (height 10.7 mm); 14, Trento, S-side Plattkofel (Sasso Piatto) 9 km SE of Ortisei, 2200-2300 m alt., E.G. leg. (height 10.4 mm). 15, C. d. huettneri, Austria, Niederösterreich, SW-side Schneeberg, Weichtal, 600 m alt., E.G. leg. (height 13.2 mm). 16, 17, two conspicuously diverging forms of C. dubia, known from the Val di Funes, collected at 900 and 1600 m, respectively (12.2 x 2.8 mm and 11.4 x 3.2 mm, respectively). Photographs by Bank.

refer as locality data "Helvetia?" and "Bern?". The lectotype (design. Forcart, 1957: 193, pl. 3 fig. 19) and two paralectotypes belong to *C. d. dubia*. Two more paralectotypes belong to *C. b. bidentata* (Ström, 1765); these specimens were also classified with *C. dubia* by Forcart (1957: 185). It remains unclear why Nordsieck (1990: 145, footnote) considers *G. (C.) roscida* different from *C. d. dubia*.

We studied a paralectotype from the type locality of *C. d.* var. *obsoleta* A. Schmidt, 1856 (ZMB, no. 101710), a specimen figured by A. Schmidt (1856: pl. 5 fig. 90). This shell agrees perfectly well with the revised interpretation of *C. d. dubia*.

After the original description, the nominal taxon C. d. var. sordellii Adami, 1876, was mentioned again only by Pini (1883: 142), Adami (1886: 180, sub 'sordelliana'), and P. Hesse (1915: 32). It is not listed by Alzona (1971). In the Colln Paulucci (MZUF) we studied two samples with 3 and 15 syntypes, respectively, donated by Adami. It clearly concerns C. d. dubia.

From the Italian Alps, Pini (1883) described two 'varieties' of *C. dubia*, viz. reticulata and langobardica. The type locality of the former one is Valtellina; from that valley Adami (1886: 180) described his var. sordellii, which belong in the synonymy of *C. d. dubia*. In the Colln Paulucci a sample of eight shells labelled langobardica has the locality data "presso Erba (Brianza)", with the note "Typus". Maybe this concerns syntypes, which belong to *C. d. dubia*.

Evidently, the interpretation of the nominate subspecies of *C. dubia* by Bourguignat (1877: 18-20), Locard (1895: 90-91), Forcart (1957: 193) and Nordsieck (1990: 145) is correct, whereas that given by Klemm (1960: 82-85) cannot be accepted.

Clausilia (Andraea) dubia vindobonensis A. Schmidt, 1856 (figs 2, 7, 19)

Clausilia dubia var. vindobonensis A. Schmidt, 1856: 40, 42, pl. 5 figs 97-98. Lectotype (design. Kilias, 1974: 192): ZMB 101728 (the specimen figured by A. Schmidt, 1856: fig. 97). Type locality: "Schloß Lichtenstein" [= Austria, province of Niederösterreich, Mödling, ruins of the castle Lichtenstein].

Notes.- We agree with H. Nordsieck (1990: 145) that this is the subspecies referred to as C. d. dubia by Klemm (1960). It is distributed in the E. and SE. Alps. Klemm (1960: 83) considered the "Dornbacher Park", Vienna, the type locality of C. d. vindobonensis. This is only one of the localities mentioned by A. Schmidt (1856: 42), however. The lectotype is from near Mödling (see above). We studied six paralectotypes from the type locality (ZMB 101728), all of them clearly consubspecific (fig. 2).

(2) A neglected, alpine subspecies from the southeastern Alps in Italy

The so-called variety alpicola Clessin, 1878, of *C. dubia* is poorly known. Klemm (1960: 106) only emphasized that it is not identical with any taxon known from Austria. Apart from a simple figure published with the original description, the form has never been depicted. We propose to use the name *C. d. alpicola* for a grouping of rather heterogeneous populations which might have evolved on pleistocene nunataks.

Clausilia (Andraea) dubia alpicola Clessin, 1878 (figs 10-14, 18, 20)

Clausilia dubia var. alpicola Clessin, 1878: 86, pl. 3 fig. 14. Syntypes lost. Type locality: "Schlern in Südtirol 2560 m" [= Italy, province of Bolzano, Schlern mountain or Monte Sciliar, at 2560 m altitude].

Description and differentiation. — Shell relatively small, light yellowish brown, slender fusiform, with somewhat flattened whorls. Teleoconch densely sculptured with very fine radial riblets, c. 11/mm on the penultimate whorl. The sculpture may be more or less obsolete. Columellaris low, slightly notched in front. Shell width 2.6-2.9 mm; height 9.4-13.2 mm.

Shells of C. d. dubia from northeastern Italy (figs 8-9) differ most conspicuously by coarser radial riblets, c. 7/mm, and slightly more convex whorls. They reach somewhat larger dimensions and are darker brown in colour.

Records (fig. 18). — BELLUNO. QS10: Mte. Pavione (Venmans, 1959: 364, sub dubia; NNM-V 8387/4, 8388/4). QS15: between Arabba and Passo Pordoi (Kofler & Kollmann, 1974: 141, locality 159, sub dubia; FSM 36-89). QS24: between Malga Ombretta and Malga Ciapela, 2000 m (NNM-V 6444/3). QS31: Pian Eterno (= N. Mte. Pizzocco, W. Lago del Mis) (Venmans, 1959: 364, sub dubia = NNM-V 8400/1). BELLUNO/TRENTO. QS11: le Vette (Venmans, 1959: 364, sub dubia = NNM-V 8392/9). QS15: Passo Pordoi (VENMANS, 1954: 74, sub dubia = NNM-V 6315/1). QS24: Passo di Fedáià, 2000 m (Venmans, 1954: 74, sub dubia = NNM-V 6314/2). Without UTM-code: Marmolada (Venmans, 1954: 74, sub dubia = NNM-V 6136/2). BOLZANO. PS95: "Schlernbödele Hütte" SE. Siusi (NNM/1). QS05: Sasso Piatto (Kofler & Kollmann, 1974: 137, locality 145 [partly], sub dubia cf. obsoleta = FSM 36-83). BOLZANO/TRENTO. QS05: S-side Sasso Piatto, 2200-2300 m (NNM/9). QS15: Passo di Sella (Kofler & Kollmann, 1974: 138, Fundort 148, sub dubia cf. tettelbachiana = FSM); S-side Sasso lungo (Kofler & Kollmann, 1974; 139, locality 150, sub dubia obsoleta = FSM 36-101). TRENTO. QS00: between Passo del Brocon and Castello Tesino, near the 'Albergo Mte. Agaro', 1630 m (RBH). QS03: between Predazzo and Moena (NNM/5). QS05: Campitello di Fassa, Friedrich Augustweg along the Sasso Piatto, 2200-2350 m (NNM/31). QS13: Passo di Rollo, near 'Kehre 21', 1276 m (NNM/12). QS15: Penia (Venmans, 1954: 74, sub dubia = NNM-V 6313/1); E-side Passo di Sella, 3.5 km NNE. of Canazei, 1900 m (NNM/13); 5 km E. of Canazei (Richtung Passo di Fedaia), 1900 m (NNM/3); Alba, 1500 m (NNM/3).

Notes. — Populations with narrowly sculptured, rather small shells of *C. dubia*, with a low, simple columellaris, are distributed at altitudes over 1200 m in the Dolomites of N. Italy. Records from outside that range (e.g. Tschapeck, 1883, 1887; Grossu, 1981: 179) apply to other taxa. This strictly alpine, endemic form of the Dolomites apparently occurs in an area from which other taxa with an alpine, relict character, like *Ananta stenzii* (Rossmässler, 1835), are known. Maybe such taxa are the descendants of molluscan populations which survived and differentiated in that area on pleistocene nunataks as glacial refuges. As becomes obvious from figure 20, the records of *C. d. alpicola* are situated on or near former nunataks. Only in the north *C. d. alpicola* has post-glacially invaded over short distances areas once covered by pleistocene glaciers.

In northeastern Italy, C. d. alpicola and C. d. dubia are clearly differentiated. Hybrid populations or hybrid zones have not been located. Elsewhere in the vast range of the species there may be local forms however, that are morphologically similar to C. d. alpicola. The forms of C. dubia occurring in the Val di Funes (see the next chapter) are clearly different from C. d. alpicola, although these populations live close to its northernmost localities.

There are no syntypes of *C. dubia alpicola* in the collection of S. Clessin, which is kept in the Staatliches Museum für Naturkunde, Stuttgart (H.-J. Niederhöfer, personal communication). Syntypes are also lacking in the other collections that were studied with respect to *C. dubia*. Because the taxon in question can be identified reasonably well by

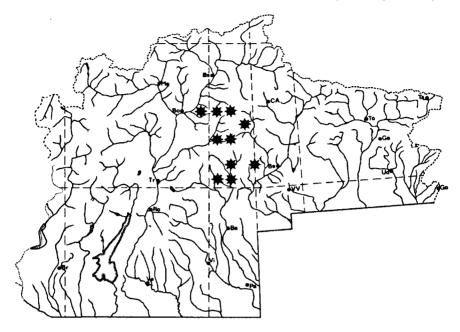


Fig. 18. Records of C. d. alpicola in NE. Italy.

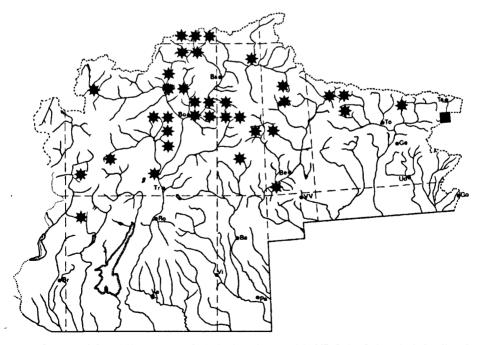


Fig. 19. Records of C. d. dubia (stars) and C. d. vindobonensis (square) in NE. Italy. Only a single locality of C. d. vindobonensis in NE. Italy is known: Udine, Cave d. Predil, 1950-1150 m (UM94) (WNH; also mentioned from this locality by M. von Gallenstein, 1852: 92 – sub C. gracilis).

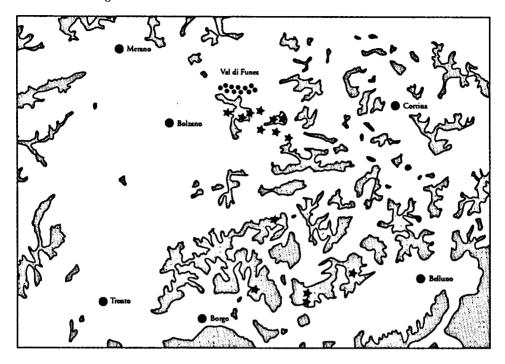


Fig. 20. Records of *C. d. alpicola* (stars) in NE. Italy, plotted on a map (1:1,000,000) indicating (in white) the areas that were permanently glaciated during the LGM (= Last Glacial Maximum: Würm) (based on Van Husen, 1987). The location of the Val di Funes, NE. of Bolzano, is also indicated.

the combination of its originally reported morphological characters and its type locality, there is no need to select a neotype.

C. dubia alpicola has an island-like range (figs 18, 20) amidst populations of C. d. dubia. To demonstrate this, the records of the nominate subspecies in northeastern Italy (fig. 19) are also listed.

Records of C. d. dubia. — BELLUNO. QS24: Serrai di Sottoguda, 1275 m (RBH). QS25: W. Mte. Pore, E-side Andraz, 1300-1400 m (NNM). TM74: between Fusine and Staulanza (Kofler & Kollmann, 1974: 141, locality 162 = FSM 36-94); gorge E. of Caprile, 1025 m (NNM). TM86: Val Fonda (Kofler & Kollmann, 1974: 143, locality 196a = FSM 36-80; WFW). UM16: Entrance Valle Visdende, up to 1350 m (Schrott et al., 1973: 53); westbank Torrente Digon, 2,5 km N. of Capella di Tamai (N. of Sega Digon), 1500 m (Bank, 1985: 69). UM25: R. Enghe, 1600 m (Schrott et al., 1973: 53); between Monte Siera and the rockface above the Rifugio Monte Siera (Schrott et al., 1973: 56). UM26: "Gosse", 1750 m (Schrott et al., 1973: 55); Cima Sappada (Schrott et al., 1973: 56, 57); between Val Sesis and 'Käser Kreuz' (Schrott et al., 1973: 58); from 'Käser Kreuz' up to 1900 m (Schrott et al., 1973: 58); Val Sesis (Schrott et al., 1973: 59); Sappada (FSM 36-108). BELLUNO/UDINE. UM25: Passo Siera (Schrott et al., 1973: 54). BOLZANO. PS17: Burgusio (Strobel, 1855: 165). PS55: Val d'Ultimo, some localities from 400 to 2000 m" (Schrott, 1947: 59). PS65: Passo d. Palade (Strobel, 1851:

30). PS65: Tesimo, 600-1500 m (Schrott, 1939: 41 = FSM 36-78). PS67: Merano (Strobel, 1855: 165); Passo (Schrott, 1933: 92). PS68: Malga di Stulles (Schrott, 1933: 92); PS77: gorge Masul (Schrott, 1933: 92); Pico Ivigna (Schrott, 1933: 92); Viadacqua (Schrott, 1933: 92). PS79: Racines (Schrott & Kofler, 1972: 407 = FSM 36-92); "Telfer Weißen" (Schrott & Kofler, 1972; 407); Giovo (Schrott & Kofler, 1972; 407); between Mareta and Ridanna (Schrott & Kofler, 1972: 407); Ridanna, direction "Mareiter Stein" (Schrott & Kofler, 1972: 407); "Mareiter Stein", 2192 m (Schrott & Kofler, 1972: 407). PS85: southern Valle Sarentina (Schrott, 1936: 310). PS86: Valle Sarentina (Strobel, 1855: 165). PS89: Vipiteno (Schrott & Kofler, 1972: 407); Prati (Schrott & Kofler, 1972: 407); castle Tassol (Schrott & Kofler, 1972: 407; HMK); "Gilfenklamm" (Schrott & Kofler, 1972: 407; HMK); castle Pietro (Schrott & Kofler, 1972: 407); Pruno (WFW); Pruno, road to Passo di Pennes, 1100 m (WNH); between Casateia and Vipiteno, 960 m (WNH), PS95: Castelyecchio (FSM 36-102), PS96: between Chiusa and Monasterio di Sabiona, 500 m (RBH). PT70: "Kogbachwasserfall" near Fleres (HMK). PT80: Colle Isarco (Schrott & Kofler, 1972: 407); Valmigna (Schrott & Kofler, 1972: 407). PT90: Brennero (Strobel, 1855: 165). QS05: Pan de Confin s. San Christina Valgardena (Kofler & Kollmann, 1974: 136, locality 144 = FSM 36-84); Sasso Piatto (Kofler & Kollmann, 1974: 137, locality 145 [partly] = FSM 36-85). QS06: Ortisei (Kofler & Kollmann, 1974: 139, locality 152 = FSM 36-97); below Ortisei (WFW). OS15: Passo di Gardena, road to Plan (Kofler & Kollmann, 1974: 139, locality 153 = FSM 36-79); Colfosco, between Plan and Corvara in Badia (Kofler & Kollmann, 1974: 140, locality 157 = FSM 36-95). QS29: Valle di Túres (FSM 36-81). TM70: Lago di Bráies, 1500 m (NNM). TM87: W-side of the road near the former 'Landro', 1400 m (NNM); 4 km S. Lago di Dobbiaco, 1300 m (WMD). BOLZANO/TRENTO. PS55: Valle Marano S. Bagni di Mezzo, "Hofmahd" (FSM 36-98). PS64: Passo d. Méndola (Strobel, 1851: 30). BRESCIA. PR08: Mte. Rondenino SSW. Passo di Croce Domini, 2000 m (Adami, 1886: 180). PS01: near Edolo, 1250 m (Adami, 1886: 180). BRESCIA/TRENTO. PS22: Mte. Tonale, 1500-2100 m (Adami, 1886: 180). TRENTO. PS51: Lago di Molveno, Alb. Molveno (WMD); Ristorante Ciclamino nnw. Molveno (WMD). PS63; gorge near San Romedio, 650 m (WNH); San Romedio, chapel, 672 m (RBA); between Sanzeno and San Romedio, 650 m (WNH). QS12: Mga. Fosse N. San Martino di Castrozzo (FSM 36-120). UDINE. UM26: Pierabec (FSM 36-105); Forni Avoltri (FSM 36-106). UM65: 2 km S. Passo di Pramollo (WFW).

(3) An alpine altitudinal (?) cline outside the range of C. d. vindobonensis

Next to some 'lowland subspecies', Klemm (1960) distinguished three kinds of populations occurring at higher altitudes, viz., 1) a subspecies restricted to high altitudes, C. d. kaeufeli Klemm, 1960, supposed to have survived glacial periods within the Alps, amidst the ice on nunataks, 2) a widely distributed subspecies, C. d. dubia [! obsoleta sensu Klemm, 1960] also known from the lowland outside the Alps and considered a postglacial invader, regionally living from the valleys up to high in the mountains without any obvious change in shell morphology (if there are no other conspecific taxa in the area), and 3) the upper part of (stepped) clines, starting from the lowland C. d. vindobonensis, via C. d. huettnen Klemm, 1960, and C. d. schlechti A. Schmidt, 1856, to the strictly high-alpine C. d. tettelbachiana Rossmässler, 1838. In these E-Alpine altitudinal clines the shells change conspicuously in size, shape and sculpture, from large, slender and prominently sculptured along the Alpine border to small, tumid and smooth at high altitudes in the adjoining Alps.

2.7-3.0 mm

2.9-3.2 mm

If the E-alpine altitudinal variation had evolved only post-glacially, without any contribution from former nunatak populations, it would be puzzling why similar forms did not evolve during the post-glacial dispersal of *C. d. dubia*. The following observation concerning altitudinal variation probably connected to *C. d. dubia*, close to the range of *C. d. alpicola*, complicates the pattern even more.

From a valley in the Italian Alps, the Val di Funes (Villnösstal), we studied six samples of *C. dubia*, collected independently at three occasions between 700 and 1600 m altitude over roughly a transect of c. 10 km. Each sample is not particularly variable, but mutually most samples are strikingly different. Maybe this concerns an isolated case of clinal variation in *C. dubia*, comparable to that known from the eastern Austrian Alps, but different in various aspects. The shell measurements of the samples are indicated in table 1. At 700 m the shells are very slender and clearly sculptured; this form is similar to ribbed *C. d. huettneri* from the Schneeberg area in Austria. Somewhat higher, at 900 m, the shells are still rather slender, but slightly smaller and smooth (fig. 16). This

altitude	n	size range shell height	size range shell width
700 m	10	12.2-15.3 mm	2.7-2.9 mm
900 m	28	10.2-13.4 mm	2.8-2.9 mm
1100 m	11	10.6-13.7 mm	2.7-2.8 mm
1200 m	61	10.3-12.7 mm	2.9 mm

10.8-12.2 mm

9.9-11.4 mm

Table 1. Variation of C. dubia in the Val di Funes

14

1400 m

1600 m

strongly reminds of the Austrian clines, in which C. d. huettneri 'looses' its sculpture at higher altitudes, becomes smaller and changes into the smooth C. d. schlechti. However, there is no C. d. tettelbachiana following higher up here. At 1100-1400 m three samples of typical C. d. dubia were found and at 1600 m a sample with tumid shells and relatively convex whorls (fig. 17), still with the characteristic, relatively widely spaced sculpture of C. d. dubia from the Dolomites, and clearly different from C. d. alpicola. More samples should be taken at various altitudes to be sure about the character of the variation. At present we can already conclude that C. dubia is more diverse in this single valley than it is in the rest of northern Italy. It might not be completely irrelevant to note that Acicula lineolata lineolata (Pini, 1884) has been reported, widely isolated from the main range of the subspecies, from the entrance of the Val di Funes at Gudon (Boeters et al., 1989: 67).

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